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Payoff- and sex-biased social learning interact in a wild primate population

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SUMMARY

Social learning in animals is now well documented, yet few studies have determined the contexts shaping when social learning is deployed. Theoretical studies predict copying of conspecifics gaining higher payoffs [1-4], a bias demonstrated in primates only in captivity [5]. In the wild, research has shown selective attention towards the philopatric sex, a group's stable

core [6]. Here we report the first rigorous experimental test of the existence of a payoff-bias in wild primates and its interaction with the sex of the model. We created a payoff bias in which an immigrant alpha male in each of three groups of wild vervet monkeys received five times more food upon opening a foraging box than did the philopatric alpha female, whereas in two control groups male and female models received the same amount of food. We tested whether this payoff asymmetry would override the previously documented selective learning from resident females. Group members were tested after having watched both models. When both models received the same amount of food, audience members copied the female model significantly more than the male model, confirming previous findings. However, when a marked payoff bias was introduced, male, but not female, vervet monkeys significantly more often copied the male model receiving a higher payoff. These results demonstrate behavioral flexibility in the dispersing sex in these primates and suggest that the philopatric sex can afford to be more conservative in their social learning. Our findings show that multiple social-learning biases can coexist and interact within the same species.

RESULTS AND DISCUSSION

Numerous species, from insects, birds, and fish to cetaceans and primates, have been shown to acquire information or skills through social learning [7-21]. Social learning is the mechanism underlying cultural transmission and individuals can use different strategies to learn socially. Learning more about the evolution and underlying mechanisms of such cultural behavior in animals can help us better understand the evolution of humanity's distinctive cumulative culture [22]. Multiple hypotheses have been proposed to investigate when and from whom individuals might be disposed to learn socially [1, 23-27]. The main distinction made is between direct (or content) biases, such as payoff-biased social learning, where attention is focused on characteristics of the observed behavior itself [23, 28, 29], and indirect (or context) biases, where individuals focus on particular individuals (for instance, they could copy high ranking

or older individuals of their group) or commonly seen behavioral variants, without directly considering the payoff of the behavioral variants. Although theoretical models would suggest that selective attention to individuals yielding the highest payoff would be the most adaptive strategy, individuals have to be able to evaluate the value of a payoff and then to make a decision according to this evaluation. Because this may be too cognitively demanding, many species may have to settle for one or more of the indirect biases, such as copying what the majority of the group do or specific group members that could predict success like older or high-ranking individuals. It is therefore important to test for the existence of a payoff-biased strategy in non-human primates. Moreover, humanity's success as a species depends on cumulative culture, and such a test could also allow us to better understand the evolution of cumulative culture, because a payoff-biased copying strategy could enable individuals to always adopt more beneficial behavioral variants, progressively enhancing their complexity.

Empirical studies in captivity have provided extensive support for context biases in social learning [23-27, 30-35]. Field observations also confirmed that certain individuals, such as kin and older individuals are specifically looked to as 'models' for social learning [36-41]. Biases towards copying dominant individuals in social learning contexts have been found in some captive primates [33-35] yet not in the only study to date in the wild [42]. Field experiments on vervet monkeys have revealed multiple social learning biases depending on the identity of the observers. Infants selectively copied their mother in both a food manipulation [39] and food choice [40] experiments. Immigrant males copied the local foraging norm in a food choice experiment despite possessing conflicting personal knowledge about what was the palatable and the unpalatable option [40]. Members of the philopatric sex (in the case of vervet monkeys, females) were more likely to be used as models in a two-action social learning task than members of the dispersing sex [6].

Some studies have reported payoff-biased social learning strategies in humans [2-4], captive chimpanzees [5], and fish [1]. Recently, Barrett and colleagues [43] described a form of payoff-biased strategy in wild white-faced capuchin monkeys. The researchers introduced a novel food item in a wild group of capuchins and observed the diffusion of extraction techniques that varied in their success rates, estimated as time needed to open the fruit. In our study, we expanded significantly on Barrett and colleagues by using multiple groups, including control groups, and a simple task in which similar actions could lead to variation of rewards. Thus, we explicitly tested for the presence of a payoff-bias strategy and a potential interaction between social learning strategies, in a species of Old World monkey.

Testing the existence of payoff-biased strategies in a wild population of primates allows the discovery of whether they possess the cognitive abilities enabling them to make these adaptive choices, despite the diversity of information in their natural environment. Discovering whether such strategies operate in wild populations offers important progress in the study of cultural transmission. Mechanisms of social learning may be more deeply understood, by further identifying how individuals make decisions to learn socially.

In our experiment, we explored whether payoff-biased social learning operates in wild vervet monkeys and whether it may interact with, or override, the female-directed selective attention previously demonstrated in this species [6]. Vervet monkeys live in multi-male, multi-female groups. Females reside in their natal group for their entire life and form a linear dominance hierarchy with a stable matrilineal social structure [44-46]. Adult females and their offspring therefore form the core of the social group. Inbreeding is avoided through males dispersing into new groups when they reach sexual maturity (around 4-5 years old) and moving several times throughout their life (for more details see supplemental information).

An experimental contrast in which male models received greater payoffs than did females models (five pieces of apples vs one piece of apple) was created in three groups of wild vervet monkeys. In two other control groups, the two models received the same amount of food (one piece of apple). The artificial foraging box used during the demonstration phase had a door at each end with a separation in the middle (Fig.1), (see video S1 and S2 in supplemental information for more details). One side of the box was painted black and the other side white. The doors of the box were locked by an electric magnet that could be deactivated remotely by an experimenter when the desired social model was approaching. Wherever possible, the highest ranking male and female in each group were trained as models (7 cases), but where this individual was unwilling to approach the box, we trained the individual immediately below it in the hierarchy (3 cases). Each model was trained to come to ‘their’ side of the box, either black or white, to extract a food reward (Table 1). Colors were counterbalanced across the different experimental groups. During the demonstration phase both models opened the box one hundred times to ensure that most group members had watched them. The experimental phase began directly after the demonstration. We offered boxes that looked the same but with both doors unlocked and lacked a separation in the middle, so every monkey could have access to both sides of the box (see video S3 in supplemental information for more details). Successful participants gained access to one single piece of apple placed in the middle of the box to avoid competition, this in both payoff-bias and control contexts. During this experimental phase we recorded which side monkeys approached and manipulated first, to see if they would choose first the female side or instead copy the model with the highest payoff, i.e. the male.

Vervets preferentially copy females so long as payoffs of males and females is similar

The first manipulation made by the monkeys is the most important one, as individual learning can influence subsequent choices. We therefore focused on the first choice made by group members in our analyses. We recorded a total of 65 individuals manipulating the box (Payoff-

bias condition: 42 participants; Control condition: 23 participants), (see Table 1).

As van de Waal and colleagues had reported for another population of wild vervet monkeys [6], we found that individuals preferentially copied the female model in the control condition, when female and male models received the same amount of food out of the box (proportion tests $\chi^2 = 5.261$; $n=23$ $p = 0.022$; fig.2a). However, in the condition where males obtained greater rewards, there was no evidence that across all individuals, monkeys preferentially chose one side of the box first (male side or female side). Instead, they copied both sides equally (proportion tests $\chi^2 = 0.857$; $n=42$; $p = 0.355$; fig.2b). (See also supplemental results).

Biased attention does not explain the first choice made

One might expect the above result to be influenced by biases in visual attention. However, we found no correlation between the first choice individuals made and the side they had watched the most being opened during the demonstration phase by models, or was chosen during the experimental phase by any another individual, whether in payoff-bias or control conditions (One-tailed Spearman correlation: Payoff-bias: $r = -0.091$; $n=42$; $p = 0.566$; Control: $r = 0.026$; $n=23$; $p=0.907$, $N=23$). Thus, we found no evidence that individuals chose to preferentially copy the female or male model depending on how often they had attended to one model or the other. These results suggest that either the model's identity or the quantity of food extracted from the box was more important for the monkeys' decision-making than the amount of experience they had gathered of a specific side being open during the demonstration phase. (See also supplemental results).

Sex of observer monkeys also influenced their first choice

Using Generalized Linear Models (GLM), we controlled for the influence of several participant characteristics, namely sex, age, rank, group identity, and kinship (degree of relatedness) with

the female model and with the male model. Results showed that in the payoff-bias condition where the male model received a greater reward than the female model, males tended to copy the male model more, whereas females copied the female model more (GLM, $n=42$, $p=0.005$; fig.3a & Table 2). However, this effect did not occur when female and male models obtained the same amount of food (GLM $n=23$, $p=0.683$; fig.3b & Table 2). Indeed, when analyzing the choice made by male participants only, we found significantly more males copying male models in the payoff-bias condition than in the control condition (proportion test $X^2= 6.250$; $n=16$, $p= 0.012$). By contrast we found no difference in the number of males copying the female side depending on the experimental condition (proportion test $X^2= 0.059$; $n=17$, $p= 0.808$). Turning to the choice made by female participants, we found that the experimental conditions had no influence on the choice of the females (proportion test, when females copied the female models: $X^2= 2.130$; $n=23$, $p= 0.144$; when females copied the male models: $X^2= 0.500$; $n=8$, $p= 0.480$). We found no significant influences of the other factors included in our model (age, rank, group, kinship with female model, and kinship with male model) for either the experimental condition or the control condition (Table 2). (See also supplemental results).

Our most striking and novel finding is that if potential male models are seen to gain greater payoffs than resident females, who are normally the preferred models for social learning, male vervet monkeys copy the more successful male model significantly more often than in the control condition, whereas female monkeys persist in copying the female model despite her lower success. That a payoff bias can override the normal selective attention of male vervet monkeys toward female models suggests greater flexibility in the social learning rules of the dispersing sex in this species. More generally this implies that a monkey is capable of using multiple social learning strategies in combination, contingent on the conditions that the individual is exposed to.

Our results thus reveal an interaction between as many as three variables influencing vervet monkey decisions about social learning: pay-offs obtained by potential models, the sex of the model, and the sex of the observer. Such complex contingencies may be explicable by the behavioral ecology of vervet monkeys. First, as the males are the dispersing sex in this species, they might benefit from greater behavioral flexibility than females because they have to integrate into a totally new group when they migrate. Such dispersal is a very difficult period marked by a number of potentially risky situations. Upon leaving the safety of their natal group, males must quickly find a new group to join, as a lone monkey is more vulnerable to predators. Then on immigration, males are often threatened and injured by the individuals (males or females) from the new group [46-48]. They typically begin life in their new group as low rankers [47, 49]. Thus, to integrate into a new group, being able to behave flexibly may be adaptive, especially with regard to social learning rules. Such flexibility would enable integrating individuals to adopt the most efficient strategy to learn from others depending on the situation, and by copying the most successful individual, they may adopt the most beneficial behaviors. Learning socially the habits of the males when gaining a higher reward might also increase the survival and fitness of integrating males by copying their rivals when successful. Accordingly, we would predict that in species where females are the dispersing sex, as in chimpanzees [50], the sex effect would be reversed.

A previous study on the same vervet monkey population revealed that after dispersing, males were prepared to flexibly abandon their own earlier, experimentally induced preference for one of two alternative colors of provisioned corn for the one preferred by their new group [40]. Thus, dispersing males appear to respond more to their social knowledge than their earlier personal experience concerning food choice. The results of this study indicated a disposition for conformity in the males, in that they abandoned their habitual preferences in favor of those of a majority of others feeding in their new group [40]. Critics have argued that assuming

conformity may be premature, because immigrant males might be using other rules such as copying the most high-ranking individual in the group [51]. However, this latter explanation has recently been tested, with negative results [42]. The present results provide support for the presence of bases of social learning that may complement conformist biases in dispersing males and provide adaptive forms of behavioral flexibility.

Female vervet monkeys did not exhibit the same behavioral flexibility as males. For females, in a species where they are the philopatric sex, it may be more adaptive for them to behave relatively conservatively, maintaining close and strong bonds with the other philopatric females in their group, and to be less disposed to copy immigrants unlikely to have an efficient local feeding behavior. A positive influence of bonding on females' fitness and their infants' survival has been well documented in baboons, in which females are also philopatric [52, 53]. Indeed, female philopatry is common in Old-World monkeys and our findings may be found to generalize to many other such species [54, 55]. In vervet monkeys, the only reported case of females leaving their natal group was when a group became too large for the available resources and a sub-unit of low-ranking females fissioned from the main group, starting a small splinter group [56]. A study employing the same colored corn tests revealed that splinter females showed a 100% fidelity to the color preferred by their origin group, despite being in a new social unit, and in a new home range, and prior experience that both colors were now palatable [56]. This emphasizes the constancy and conservatism of behavior in female vervet monkeys; our current findings are highly consistent with this.

Our results emphasize the flexible social learning strategies of the dispersing sex in this species of primate, whereas the philopatric sex appears to be more conservative. More generally, our study reveals that multiple social-learning biases may interact within the same species depending upon characteristics of the learner and the conditions to which they are exposed. Sex differences in social learning have also begun to be reported in both human children [57, 58]

and adults [59]. The interplay between multiple social learning rules has begun to be investigated in developmental psychology [60, 61]. However, our experimental study is explicitly testing for, and highlighting, such complexities in non-human primate behavior, and it does so in the wild, where primates are embedded in a multitude of complex decisions about such factors as foraging, predator avoidance, mating and social relationships from moment to moment. We may only now be beginning to appreciate not only the pervasiveness of social learning among animals [12, 62], but also some of the complexities of their adaptive social learning biases.

STAR ★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information includes supplemental statistical results including two tables, and three videos of the experiment.

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AUTHOR CONTRIBUTIONS

E.W., A.W. and C.S. designed the experiment. A.B. conducted the experiments, ran the statistical analyses and wrote the first draft. E.W., A.W. and C.S wrote the second draft. E.W. was granted the funding for data collection. F.E. and A.S. ran the genetic analyses. M.K. supervised the genetic analyses and commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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FIGURE LEGENDS

Fig. 1 Experimental design. a) adult female opening on the white side of the box, b) adult male opening on black side of the box. Photographs copyright: Erica van de Waal.

Fig. 2 First Manipulation. Number of individuals who chose the female side or male side as their first choice depending on the experimental condition: a) Control, b) Payoff-bias favoring males. The letter codes (AK, KB, BD, LT, and NH) represent the name codes of the different experimental groups, and the delimitations on each histogram represent the number of participants in each group.

Fig.3 Influence of the sex of participant on the first manipulation. Proportion of side chosen first, depending on the sex of the participant according to experimental condition: a) Control, and b) Payoff-bias; The letter codes (AK, KB, BD, LT, and NH) represent the name codes of the different experimental groups. AK and KB represent the two controls group, and BD, NH and LT represent the three payoff-bias groups.

TABLE LEGENDS

Experimental context	Group name code	Group size	Number of participants	Female model	Male model
Payoff-bias	BD	43	19	W	B
	LT	30	10	B	W
	NH	47	13	W	B
Control	AK	20	15	B	W
	KB	12	8	W	B

Table 1. Participants. Number of individuals who participated in the experimental phase, out of the total number of individuals in each group excepting infants (younger than 1 year old) as infants did not participate in the experiment (group names: BD = Baie Dankie, LT = Lemon Tree, NH = Noha, AK = Ankase, KB = Kubu). Distribution of color sides for each model is shown in the female and male model columns with W=white side of box; B=black side of box.

Dependent Variable= side chosen first	Fixed factors	Test value (Type III)	F value	ddl	P Value
Payoff-bias context	Sex	1.927	9.887	1	0.005**
	Age	0.175	0.897	1	0.354
	Rank	0.004	0.022	1	0.883
	Kinship male model	0.349	1.791	1	0.194
	Kinship female model	0.064	0.330	1	0.571
	Group	0.735	1.885	2	0.176
Control context	Sex	0.036	0.174	1	0.683
	Age	0.068	0.329	1	0.576
	Rank	0.069	0.333	1	0.573
	Kinship male model	0	.	.	.
	Kinship female model	0.124	0.599	1	0.452
	Group	0.067	0.326	1	0.577

Table 2. Testing multiple factors influence on first choice. Summary of results of the GLM Models with all dependent variables, fixed effects, and interactions. The first GLM model analyzed the effects of the sex, age, rank, group or kinship with male model and kinship with female model, of the participants on the first choice participants made in the context of payoff-bias. The second GLM model analyzed the effect of the sex, age, rank, group or kinship with male model and kinship with female model, of the participants on the first choice participants made in the control condition. Significant differences are indicated by ** $p=0,005$.

STAR ★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Erica van de Waal (erica.vandewaal@unil.ch).

- EXPERIMENTAL MODEL AND SUBJECT DETAILS

All five studied groups (Ankhase, AK; Baie Dankie, BD; Kubu, KB; Lemon Tree, LT; Noha, NH), are part of IVP (Inkawu Vervet Project). They are wild monkeys, habituated to the presence of human since the start of the project in 2010. During the study, not counting infants, the group AK included 20 individuals (2 adult males, 4 adult females, and 14 sub adults and juveniles); the group BD included 43 individuals (4 adult males, 11 adult females, and 28 sub adults and juveniles); the group NH included 47 individuals (5 adult males, 13 adult females, and 29 sub adults and juveniles); the group LT included 30 individuals (4 adult males, 9 adult females, and 17 sub adults and juveniles); and the group KB included 12 individuals (1 adult male, 6 adult females, and 5 sub adults and juveniles). Each individual was identified using facial characteristics and natural ear-notches, or artificial ones made during captures for genetic purposes. Monkeys were named with letter codes. Regularly updated recognition files with portrait photographs and specific individual feature descriptions were constructed for each group.

Ethics guidelines: We adhered to the “Guidelines for the Use of Animals in Research” of the Association for Study of Animal Behaviour. Our experiments were approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa; and by the funders. The setup of this

experiment could involve opportunities for competition over food. However, we offered either several boxes at the same time or a single box for isolated individuals in order to minimize conflicts. We also kept the amount of food provided in every session relatively small during both phases of this experiment.

- METHOD DETAILS

- Study site

Experiments were conducted at the Inkwavú Vervet Project (IVP) between 17th of February 2016 and 21st of July 2017 on five groups of wild vervet monkeys (*Chlorocebus pygerythrus*). IVP is located in « Mawana », a private game reserve of 10,000-hectares, in KwaZulu Natal, South Africa (S 28°00.327 ; E 31°12.348). The reserve is mainly used as a hunting farm but a portion of the land is reserved for the study of vervet monkeys. The vegetation is classified as Savannah biome characterized by areas of grasslands with dispersed singular or clusters of trees, with the typical savannah thornveld, bushveld and thicket patches [63]. The reserve is inhabited by all the usual savannah mammals, except for black rhinoceroses, buffaloes, cheetahs and lions. Therefore, vervet monkeys can face their main potential predators: leopards, hyenas, jackals, pythons, cobras, mambas, puff adders, baboons, and different raptors [64].

- Hierarchy

Females were considered adult when they gave birth for the first time; males after their first dispersal. Females are philopatric. Males disperse several times throughout their lifetime. They occupy the lowest rank when they first arrive in a new group but this can change depending on the relationship they establish with the females. Otherwise vervets exhibit a linear dominance hierarchy [65, 66]. Rank in females is inherited, with the youngest female offspring acquiring the rank directly below that of her mother and the older female offspring following in rank. Whilst the male hierarchy changes depending on migrations, strength and acceptance by

females, the female hierarchy is relatively stable [56], including in this population [42]. Males and females have separate hierarchies [65]. In order to identify the rank of each individual, hierarchy analyses were run [67] using the R package ‘EloRating’ [68] for adult males and females separately, with conflict data collected ad libitum from the groups.

– Kinship

In order to assess the kinship between individuals, we calculated the degree of relatedness. Tissue samples were obtained when individuals were trapped and anaesthetized in order to be provided with a radio collar, while fecal samples were collected on a regular basis since the beginning of 2013 during weekly follows. When an identified individual defecated, parts of the feces were collected and stored according to the established sampling protocol (<http://www.aim.uzh.ch/de/research/orangutannetwork/gsp.html>). Samples were dried and stored in the field station in South Africa, before being sent to the University of Zurich, Switzerland, for analyses.

We extracted DNA using Quiagen’s DNeasy and QIAmp Stool Mini kit following the manufacturer’s protocol, with the following modifications. For each sample, 85mg to 180mg of feces were weighed and mixed with 1.7µl of Buffer ASL and 5 µl of Proteinase K and subsequently incubated in the overhead rotator overnight at 55°C. An additional 1.5µl Proteinase K was added to both fecal and tissue samples after one night of incubation, followed by overhead rotation for an additional hour. For fecal samples, the centrifugation time after addition of the InhibitEx tablet was increased to 8 min in order to stabilize the pellet. Fecal samples were further processed with the QIacube robotic workstation (Qiagen) and the concentration of all samples was measured with the NanodropR-100 (Software 3.3).

In order to estimate kinship between individuals, we calculated dyadic relatedness (r) using 17 autosomal microsatellite loci [69]. As the choice of the most accurate estimator depends on

inherent population structure and history [70], we used the program Coancestry 1.0.1.5 to determine the best performing relatedness estimator (*i.e.*, high precision and low standard deviation). We included all adult individuals plus all juveniles who took part in the experimental procedure, totaling 172 individuals. For seven different relatedness estimators, we simulated 1,000 pairwise relatedness values (r -values) for unrelated dyads (expected $r = 0$), half-siblings ($r = 0.25$), full-siblings ($r = 0.50$), and parent-offspring ($r = 0.50$), using allele frequencies obtained from all 172 genotyped individuals. Based on this analysis, we found dyadic likelihood estimator MEst [71] to be the best performing.

– Data collection

The field experiment was conducted by AB, alone or with the help of one or two other staff members of the Inkaw Vervet Project (IVP). Prior to the experiment, each staff member had to pass an identification test, assessing their ability individually recognize all monkeys of the studied group. All observers also had to pass an inter-observer reliability tests to ensure high consistency in data collection. Experiments were mainly conducted in winter because natural food resources being less abundant at this time of the year, monkeys were more motivated to participate. Experiments took place in five different groups, three groups with the payoff bias in place (Baie Dankie group, Noha group and Lemon tree group) and two control groups (Ankhase group and Kubu group).

– Training

We first trained our models, the dominant male and the dominant female of each group, to open their side of the box, either black or white side. The colors were counterbalanced across the different experimental and control groups. When the alpha female or male was too shy to

participate and get trained, we trained the next-highest ranking individual. In group KB the second female in the hierarchy was the model (daughter of the alpha female). In group LT, the model was the female of the second matriline of the group (as the females from the alpha family were too shy to approach the experimental setup, even during the experimental phase, perhaps because this group is less habituated to humans than the other groups); this female was still high ranking and had the 4th position in the hierarchy order (out of 9 adult females in total). In NH, the second female was the model; she was the sister of the alpha female. For all the other groups, male and female models were the alpha individuals.

The food reward given inside the box was one piece of an apple that all monkeys were already used to eating in other experimental settings. One apple was cut into 20 pieces, so one piece at the time was given to the monkeys, and in payoff-bias condition only male models got five pieces of apple instead of one. We always used apples of the same size in each particular session, to have regular sized pieces, and in each session, both models were trained. Except for the alpha male in the group KB, for who we had to use pieces of corn as a reward, in order to motivate his participation in the experiment, because he was not willing to participate with apples. The reward for both models in this group and for participants to the experiment was five pieces of corn.

During the demonstration, we recorded the attentional state of group members around the box. An individual was considered as attending if it was inactive and had its head and body oriented towards the model opening the box in a 10m radius of the demonstration.

– Experimental phase

The experimental phase started when a minimum of two-thirds of the group had seen both models opening the box. Following this rule, we fixed the numbers of opening for each model

to 100 times. During both the demonstration and experimental phases, once the box was opened and empty, an experimenter rebaited it.

During the experimental phase, we offered the same box. Monkeys had access to one piece of apple placed in the middle of the box (five pieces of corn for KB group to stay consistent); this in payoff-bias and control contexts, so the reward in the box could be monopolized by the monkey opening the box. All monkeys were free to interact and free to try to open the box within the constraints of the social group dynamics, such as rank. Also, in order to have as many individuals as possible trying to manipulate the box at least once, we offered the box in different ways. First, six boxes were offered early in the morning at the sleeping site, before the group started moving. But this method led to mostly high-ranking individuals accessing the boxes and monopolizing them. So, we also offered a single box to isolated individuals when the group was moving, in order to provide them with the opportunity to manipulate the box. For each manipulation of the box during the experimental phase, we recorded in the field the identity of the monkey manipulating the box, the side chosen, whether or not it managed to open the box and obtain the reward, which group members were attending the opening, and the identity of all group members within a 5 and 10 m radius of the box. All interactions with boxes were recorded using a video camera. For both phases we could perform one session per day, and a session was ended when an individual ate a total of: one apple for an adult female, two apples for an adult male, or 25g and 50g of corn for female and male, respectively.

The demonstration phase and experimental phases were done opportunistically across multiple days. The average duration of the demonstration phase was of 55 minutes, and the experimental phase session was of 70 minutes.

- QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were performed in SPSS (24.0). We conducted proportion tests in order to see if individuals choose one side preferentially during their first choice, across the three experimental phases. We calculated Spearman correlation coefficients to test for a correlation between the first choice made by participants and their attentional state (*i.e* the amount of time individuals watched each model opening its side of the box during the demonstration phase and the amount of time they saw other individuals attempting to open either side of the box during experimental phase). We also tested whether group members were attending more or not to one model or the other using a Wilcoxon paired test (see supplemental information). Then, we used Generalized Linear Models (Table 2) to control for potential effects of factors including sex, rank, kinship with male model, kinship with female model, age and group identity, on the first choice made by participants. We ran this GLM (Type III) for both the payoff-bias condition and the control condition. Side chosen first was included as the dependent variable, while sex, age, kinship, rank, and group of belonging, were all considered as fixed factors. We first ran the GLM including all interactions possible between all the factors, but since no results were significant concerning these interactions, we ran the final GLM testing only the effect of the different factors in order to retain statistical power. Finally, we conducted proportion tests in order to compare separately males and females on the effect of the experimental setup (control or payoff) on their first choice.

We had to remove one individual from our analyses (Pue) as he managed to open the box during the demonstration phase. Also in the analyses we did not take into account two males from BD (Hwa and Ubu), because they integrated into the group after the demonstration phase. Individuals younger than one year old did not participate in the experiment.

SUPPLEMENTAL INFORMATION

– Supplemental Results

Table S1. Results of Spearman correlations between the first choice made by participants and 1) the number of participants they watched opening the box (model included), 2) the last side they saw being open by a model, and 3) the last side they saw being open by the model or another participant. Related to our results “*Biased attention does not explain the first choice made*” and related to figure 2 and 3.

Table S2. First choice of individuals across the different experimental groups, when male models were more successful than female models. Related to our results “*Vervets preferentially copy females so long as payoffs of males and females is similar*” and related to figure 2 and 3.

Table S3. First choice of individuals across the different control groups, when male models and female models received the same amount of food. Related to our results “*Vervets preferentially copy females so long as payoffs of males and females is similar*” and related to figure 2 and 3.

Table S4. Testing multiple factors influence on first choice. Summary of results of the GLM Models with all dependent variables, fixed effects, with group included as random factor. The first GLM model analyzed the effects of the sex, age, rank, or kinship with male model and kinship with female model, of the participants on the first-choice participants made in the context of payoff-bias. The second GLM model analyzed the effect of the sex, age, rank, or kinship with male model and kinship with female model, of the participants on the first-choice participants made in the control condition. Significant differences are indicated by * $p=0,013$. Related to our results “*Sex of observer monkeys also influenced their first choice*” and related to figure 2 and 3.

680 – Supplemental experimental design (videos)

681 Video S1: Adult male model opening the black side of the box during the demonstration phase
682 and getting five pieces of apple.

683 Video S2: Adult female model opening the white side of the box during the demonstration
684 phase and getting one piece of apple.

685 Video S3: Sub-adult male opening the box during the experimental phase.

686

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Antibodies		
Bacterial and Virus Strains		
Biological Samples		
<i>Chlorocebus pygerythrus</i>	Inkawu Vervet Project, KwaZulu-Natal, South Africa	Erica van de Waal, University of Lausanne
Chemicals, Peptides, and Recombinant Proteins		
Quiagen DNeasy kit	QIAGEN	https://www.qiagen.com/ch/
Quiagen QIAmp Stool Mini Kit	QIAGEN	https://www.qiagen.com/ch/
Critical Commercial Assays		

Deposited Data		
Experimental Models: Cell Lines		
Experimental Models: Organisms/Strains		
Oligonucleotides		
D11S928	Wang (2006)	
D10S1483	Wang (2006)	
D1S207	Wang (2006)	
D1S244	Wang (2006)	
D1S518	Newman et al. (2002)	

D18S42	Newman et al. (2002)	
D11S1902	Newman et al. (2002)	
D5S1466	Newman et al. (2002)	
D7S2446	Wang (2006)	
D8S1106	Wang (2006)	
D12S314	Wang (2006)	
D15S108	Wang (2006)	
D18S72	Newman et al. (2002)	
D2S144	Newman et al. (2002)	
VTetra_29 F: 5'-TGGAAACCTGCAACTTCTGA-3' R: 5'-GGAAACCTGCAACTTCTGAAGA-3'	Arora (unpublished)	
VTetra_5 F: 5'-TTGCAGTGAGACAAGATCGC-3' R: 5'-GCCTGGCTCCTTTACGAGTT-3'	Arora (unpublished)	
VTri_6 F: 5'-GAGGTGGAGGTTGTAGCGAG-3' R: 5'-TAACGGCGCAATTCATACAA-3'	Arora (unpublished)	
Recombinant DNA		
Software and Algorithms		
SPSS Statistics 24	IBM	https://www.ibm.com/analytics/data-science/predictive-analytics/spss-statistical-software
Genemapper 5.0	ThermoFisher Scientific	http://www.thermofisher.com/order/catalog/product/4475073

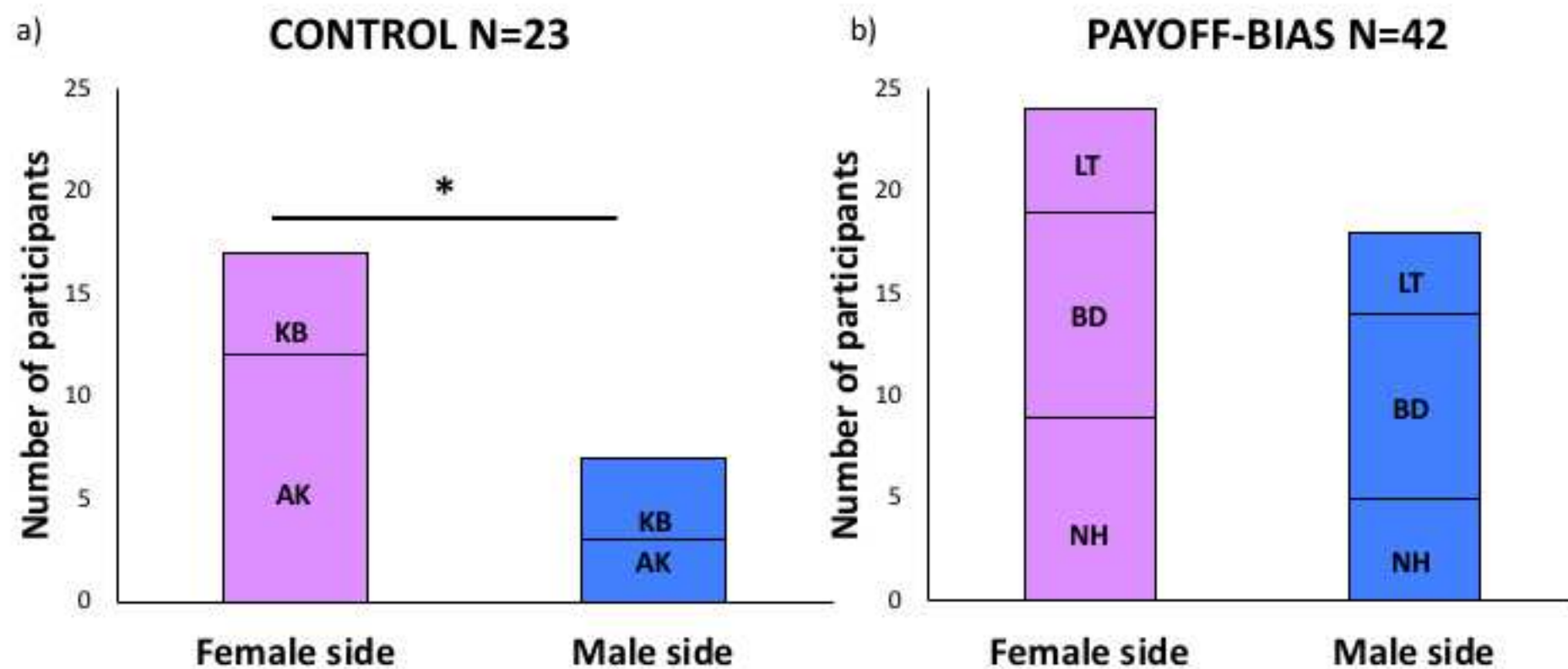
Coancestry	Zoological Society of London	https://www.zsl.org/science/software/coancestry
Cervus	Field Genetics	http://www.fieldgenetics.com/pages/aboutCervus_Overview.jsp
R (R Studio)	The R Foundation	https://www.r-project.org https://www.rstudio.com
Other		

a)



b)





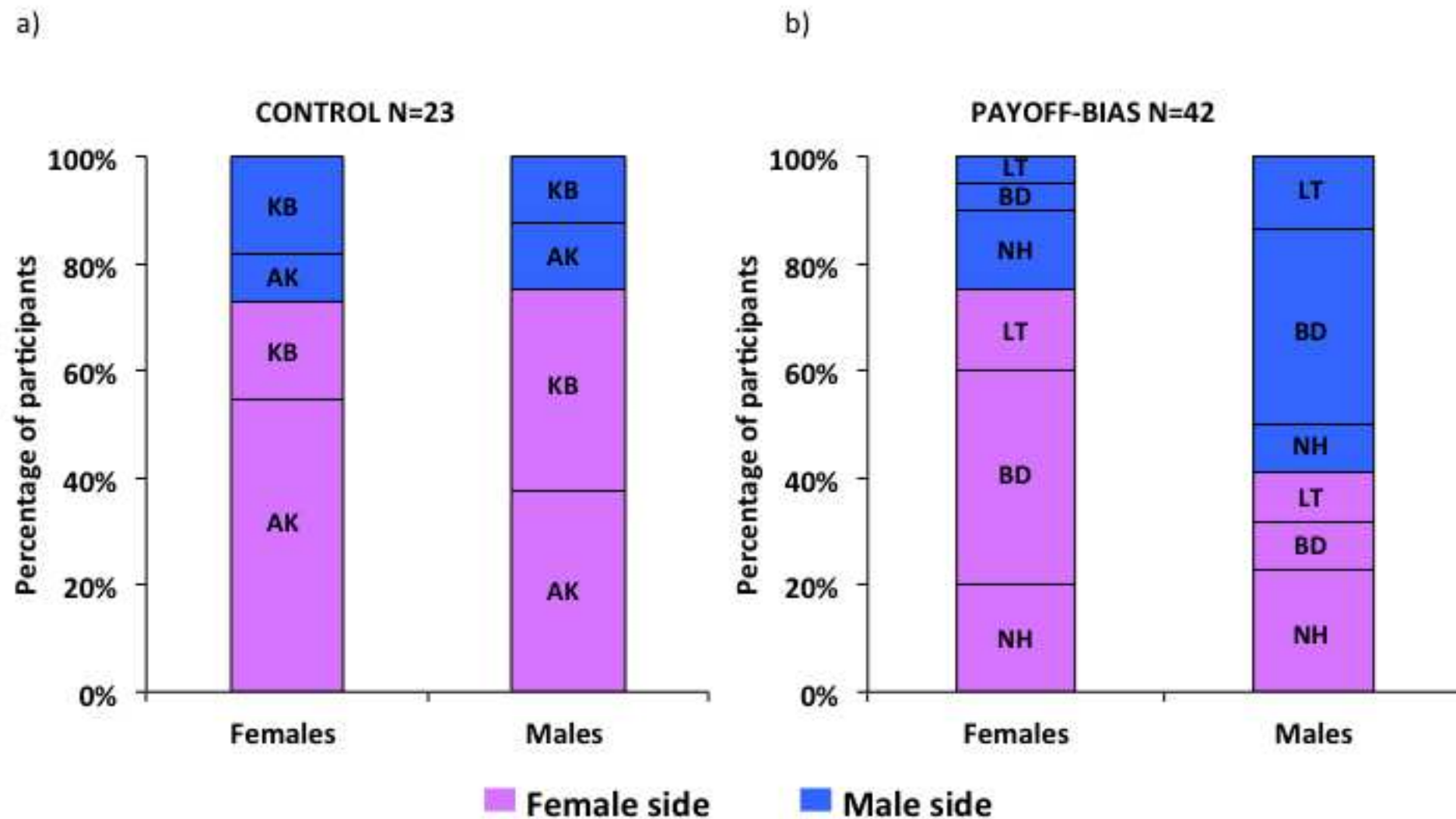


Table 1

Experimental context	Group name code	Group size	Number of participants	Female model	Male model
Payoff-bias	BD	43	19	W	B
	LT	30	10	B	W
	NH	47	13	W	B
Control	AK	20	15	B	W
	KB	12	8	W	B

Table 2

Dependent Variable= side chosen first	Fixed factors	Test value (Type III)	F value	ddl	P Value
Payoff-bias context	Sex	1.927	9.887	1	0.005**
	Age	0.175	0.897	1	0.354
	Rank	0,004	0.022	1	0.883
	Kinship male model	0.349	1.791	1	0.194
	Kinship female model	0.064	0.330	1	0.571
	Group	0.735	1.885	2	0.176
Control context	Sex	0.036	0.174	1	0.683
	Age	0.068	0.329	1	0.576
	Rank	0.069	0.333	1	0,573
	Kinship male model	0	.	.	.
	Kinship female model	0.124	0.599	1	0.452
	Group	0.067	0.326	1	0.577

Supplemental experimental design (videos)

Video S1: Adult male model opening the black side of the box during the demonstration phase and getting five pieces of apple.

Video S2: Adult female model opening the white side of the box during the demonstration phase and getting one piece of apple.

Video S3: Sub-adult male opening the box during the experimental phase.

Supplemental Results

The analyses concerning the attention of group members during the demonstration phase, also revealed that there is no correlation between the first choice made by participants in both conditions and 1) the number of participants they watched opening the box (model included), 2) the last side they saw being opened by a model, and 3) the last side they saw being opened by the model or another participant, (see Table S1).

	Spearman correlation	r	p	n
First choice Control context	1	-0.127	0.565	23
	2	-0.224	0.304	23
	3	-0.335	0.118	23
First choice Payoff-bias context	1	-0.039	0.804	42
	2	0.171	0.28	42
	3	0.266	0.089	42

Table S1. Results of Spearman correlations between the first choice made by participants and 1) the number of participants they watched opening the box (model included), 2) the last side they saw being open by a model, and 3) the last side they saw being open by the model or another participant. Related to our results “*Biased attention does not explain the first choice made*” and related to figure 2 and 3.

Also, our data showed no significant difference in the attention of group members towards male models or females models (Wilcoxon paired test: **payoff-bias** condition: $Z = -1.642$; $p = 0.101$; $n = 42$; **control** condition: $Z = -0.852$; $p = 0.394$; $n = 23$), contradicting previous results where selective attention was found only towards the female model when the experimental setup involved only one model per group [S1]. It is possible that in our specific experimental set up,

individuals became interested in the boxes, perhaps by having the dominant female involved, and then paid attention to openings by both models.

Furthermore, we controlled the females' first choice in both experimental contexts (payoff-bias and control) using a Fisher exact test (due to the small sample size) ($\chi^2 = 0.019$; $df = 1$; $p = 0.890$; $N = 31$) and we found that females did not copy the female side in the payoff-bias context significantly more than the control.

First manipulation	Female copied	Male copied	Total
NH	9	4	13
BD	10	9	19
LT	5	5	10
Total	24	18	42

Table S2. First choice of individuals across the different experimental groups, when male models were more successful than female models. Related to our results “*Vervets preferentially copy females so long as payoffs of males and females is similar*” and related to figure 2 and 3.

First manipulation	Female's side chose first	Male's side chose first	Total
KB	5	3	8
AK	12	3	15
Total	17	6	23

Table S3. First choice of individuals across the different control groups, when male models

and female models received the same amount of food. Related to our results “*Vervets preferentially copy females so long as payoffs of males and females is similar*” and related to figure 2 and 3.

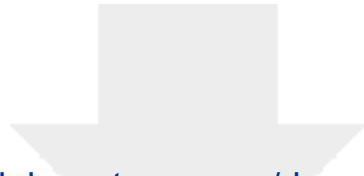
Finally, to support the results found with the GLM as illustrated in figure 2 and 3, we also conducted another statistical test to confirm that the group of belonging had no influence on the first choice made by participants. Indeed, with this test we also did not find any effect of group of belonging (control condition: Mann-Whitney U test: $U = 49.5$, $N = 23$, $p = 0.506$; payoff-bias condition: Kruskal-wallis test: $\chi^2 = 1.115$, $N = 42$, $p = 0.573$). Running the GLMs including group as random factor provided essentially the same results as in the other GLMs, see table S4.

Dependent Variable= side chosen first Random factor= group	Fixed factors	Test value (Type III)	F value	ddl	P Value
Payoff-bias context	Sex	1.500	7.169	1	0.013**
	Age	0.024	0.115	1	0.738
	Rank	0.819	3.914	1	0.059
	Kinship male model	0.424	2.024	1	0.168
	Kinship female model	0.144	0.689	1	0.415
Control context	Sex	0.029	0.534	1	0.476
	Age	0.054	0.271	1	0.610
	Rank	0.042	0.210	1	0.653
	Kinship male model	0	.	.	.
	Kinship female model	0.106	0.534	1	0.476

Table S4. Testing multiple factors influence on first choice. Summary of results of the GLM Models with all dependent variables, fixed effects, with group included as random factor. The first GLM model analyzed the effects of the sex, age, rank, or kinship with male model and kinship with female model, of the participants on the first-choice participants made in the context of payoff-bias. The second GLM model analyzed the effect of the sex, age, rank, or kinship with male model and kinship with female model, of the participants on the first-choice participants made in the control condition. Significant differences are indicated by * $p=0,013$. Related to our results “*Sex of observer monkeys also influenced their first choice*” and related to figure 2 and 3.

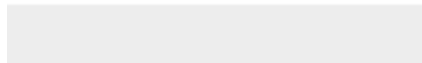
Supplemental References

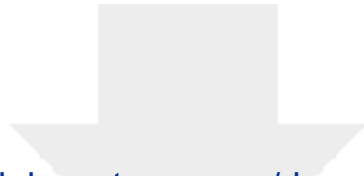
1. van de Waal, E., Renevey, N., Favre, C.M., and Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proc. Roy. Soc. Lond. B.* 277(1691), 2105-2111.



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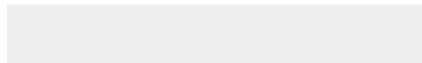
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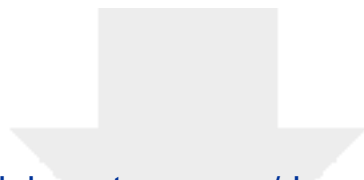




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